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LONG-TERM DYNAMICS OF BIRD COMMUNITIES IN A MANAGED FORESTED LANDSCAPE

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ABSTRACT.—I examined the long-term dynamics of wintering and breeding bird communities at the Barrens Grouse Habitat Management Area (HAM) in central Pennsylvania. I compared community structure (species richness and population abundances) among three forested sectors that varied in extent of clearcutting and among forested plot types of different age since clearcutting from 1993–95 (termed period 2). These results, which were obtained six–eight years subsequent to a third cutting cycle, were then contrasted to those from a previous study (1988–90, termed period 1). The Barrens Grouse HMA consisted of three distinct sectors: a contiguous uncut stand, a series of uncut strip corridors, and a mosaic of small (1 ha) forest patches (plots). I observed 12 wintering bird species in period 2; most species (67%) were trunk-bark foragers. Uncut plots were used more often ($P < 0.05$) by wintering birds than clearcut plots, perhaps because uncut plots contained rough-barked trees as foraging substrate and more favorable microclimatic conditions. Of the 40 breeding bird species noted in period 2, most were ground-shrub foragers occurring principally in forested corridor and patch sectors. Abundances of six ground-shrub foraging species were higher ($P < 0.05$) in the forested patch than in other sectors in period 2; these species were found primarily in recent clearcut plots. Abundances of sallier-canopy foragers were higher ($P < 0.05$) than expected in contiguous forest and forested corridor sectors in period 2. Species richness, abundances of all wintering species combined, and abundances of two foraging guilds (trunk-bark and ground-shrub foragers) were similar among sectors in periods 1 and 2 in both winter and the breeding season. Abundances of three wintering species, however, were greater ($P < 0.05$) in period 2 than in period 1. In contrast to winter, abundances of all breeding species combined, sallier-canopy foragers, and five species increased ($P < 0.05$) between periods, whereas abundance of three species declined. Significant changes in abundances of wintering and breeding birds between periods at the Barrens Grouse HMA may be explained partially by plant succession or regional trends in population abundances.
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The effect of even-aged management on abundance and distribution of bird communities has been examined in various managed forested landscapes (e.g., Crawford et al. 1981, Thompson et al. 1992, Welsh and Healy 1993). In this study, I examined the long-term dynamics of wintering and breeding bird communities at the Barrens Grouse HMA in central Pennsylvania subsequent to a third cutting cycle. My objective was to compare community structure among three forested sectors that varied in extent of clearcutting and among plot types of different age since clearcutting from 1993–95, which was six–eight years following the third cutting cycle (termed period 2). In addition, I contrasted results

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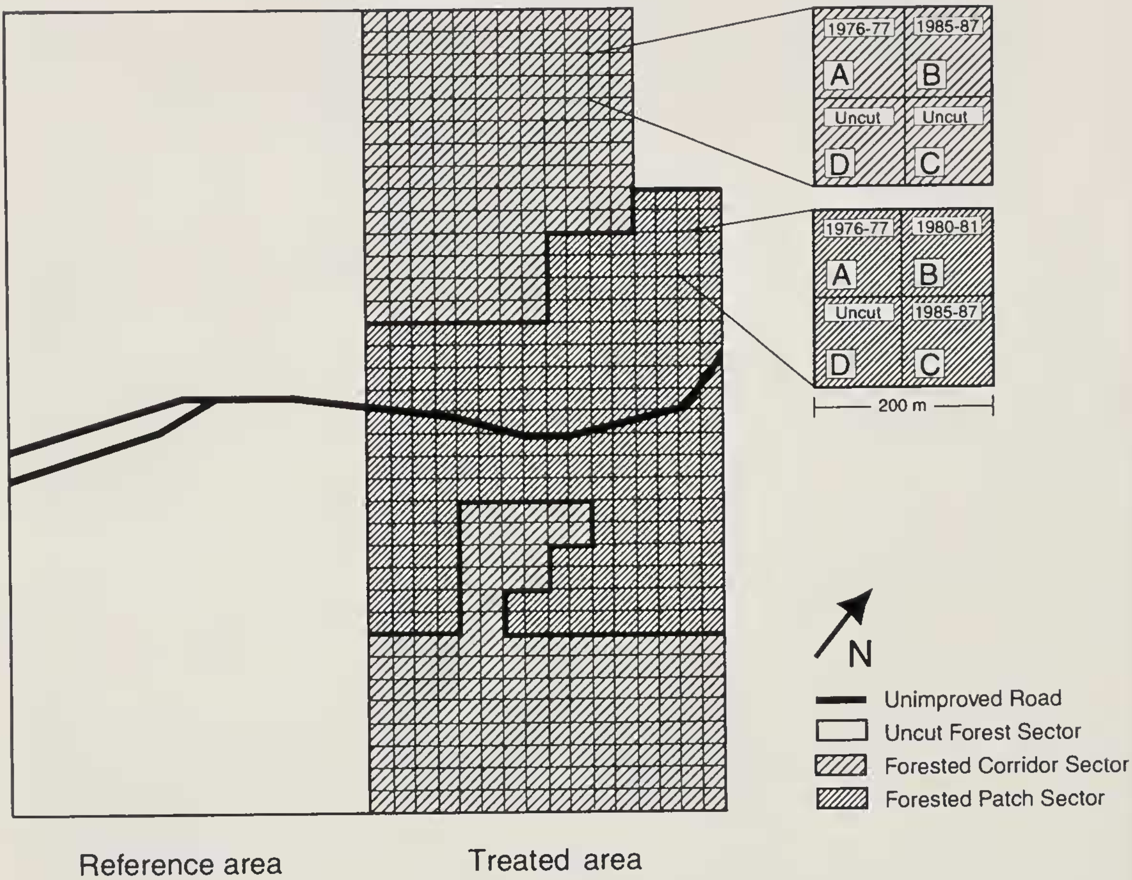

FIG. 1. Reference (contiguous forest sector) and treated (forested patch and forested corridor sectors) areas of the Barrens Grouse HMA, Centre County, Pennsylvania. Dates of clearcutting cycles (1–3) are given in plots A and B in the forested corridor sector and in plots A–C of the forested patch sector. Forest was uncut in the contiguous forest sector, in plots C and D of the forested corridor sector, and in plot D of the forested patch sector (modified from Yahner and Mahan 1996).

obtained in period 2 to those obtained in 1988–90, which was one–two years after the third cycle (termed period 1, Yahner 1993).

STUDY AREA AND METHODS

I conducted the study at the 1166-ha Barrens Grouse HMA, State Game Lands 176, Centre County, Pennsylvania, from May 1993 through July 1995 (period 2, 6–8 years subsequent to the third cutting cycle). My study site contains a reference and a treated area of similar size (Fig. 1) (Yahner 1993, 1994; Yahner and Mahan 1996). The reference area is uncut and is termed the contiguous forest sector. The treated area is separated into a forested patch and a forested corridor sector. Forest in the contiguous forest sector, in uncut plots of both forested patch and corridor sectors, and surrounding the Barrens Grouse HMA has not been cut for approximately 75–80 years.

Major overstory trees (woody stem > 7.5 cm dbh and > 1.5 m tall) on the three sectors were quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), red maple (*Acer rubrum*), and pitch pine (*Pinus rigida*). Major understory trees

TABLE 1

SPECIES RICHNESS (*S*) AND ABUNDANCE (*N*, NO./10 HA) OF ALL SPECIES COMBINED AND OF TWO MAJOR FORAGING GUILDS IN THREE SECTORS OF FOREST MANAGEMENT AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING WINTERS 1993–94 AND 1994–95 COMBINED (PERIOD 2)

	Sector			
	Contiguous forest	Forested corridor	Forested patch	Total
Species richness, *S*:				
All species combined	4	10	8	12
Trunk-bark foragers	3	7	5	8
Ground-shrub foragers	1	3	3	4
Abundance, *N*:				
All species combined	14.1	21.2	19.5	19.7
Trunk-bark foragers	7.1	18.1	15.5	15.7
Ground-shrub foragers	7.1	3.1	4.0	4.0

(woody stem = 2.5–7.5 cm dbh and > 1.5 m tall) and tall shrubs (woody stems < 2.5 cm dbh and > 1.5 m tall) were aspen, red maple, black cherry (*Prunus serotina*), and oak (Yahner 1993).

The treated area consists of 136 contiguous 4-ha blocks, with each block subdivided into four 1-ha (100- × 100-m) plots arranged in a clockwise pattern (plots A–D) (Fig. 1) (Yahner 1993, Yahner and Mahan 1996). In the forested patch sector, plot A was clearcut in winter 1976–77, plot B in winter 1980–81, and plot C in winters 1985–86 and 1986–87; this resulted in uncut forested patches (plot D) surrounded by three clearcut plots (A–C) of different ages. In the forested corridor sector, plot A was clearcut in winter 1976–77, and plot B was cut in winters 1985–86 and 1986–87. In each plot B of this sector, 15–20 overstory trees/ha were retained (Yahner 1995). This created 100-m wide corridors of uncut forest (plots C–D) adjacent to clearcut plots of two ages (plots A–B); uncut plots C and D were considered distinct from each other because proximal clearcut plots differed in age and because vegetative density near ground level was greater ($P < 0.05$) in older than in younger clearcut plots (Yahner et al. 1989). Therefore, based on age since cutting and sector, I classified the Barrens Grouse HMA into nine plot types: uncut plots in the contiguous forest sector and four plot types each (plots A–D) in forested patch and corridor sectors, respectively (after Yahner 1993).

I sampled bird communities at the same 90 1-ha plots randomly selected in a previous study (i.e., period 1) of wintering and breeding bird communities at the Barrens Grouse HMA (Yahner 1993). Of the 90 plots, 10 were in the contiguous forest sector, and 10 plots each consisted of the four habitats (plots A–D) in both forested patch and corridor sectors. Plots were representative of plots on each sector, and plot centers were located at least 50 m from disturbances, e.g., logging road, to minimize edge effects (Strelke and Dickson 1980, Yahner 1987). The minimum distance between plots was 200 m (DeSante 1986, Yahner 1993).

I visited each plot once from late December to early February during two consecutive winters (1993–1994 and 1994–95) and again in late May to late June during three consecutive breeding seasons (1993–1995). The randomized order and number of visits to plots were identical to those used in period 1 at the Barrens Grouse HMA (Yahner 1993). Visits were made between sunrise and 10:30 hr DST. After an initial 1-min equilibrium period, I noted all birds seen or heard within a 30-m radius of the center of the plot during the subsequent 5 min (DeSante 1986, Yahner 1993). I chose a 30-m radius in order to minimize edge effects at interfaces of plots in forested patch and corridor sectors (after Repenning and Labisky 1985, Yahner 1993). Birds flying through or above the canopy were not counted.

I computed two measures of avian community structure, species richness (*S*) and population abundance (*N*), for each sector and plot type based on data obtained during winters or breeding seasons combined during period 2 (Yahner 1993). Species richness (*S*) was the number of all species combined or per foraging guild; *N* was the number of contacts (no./10 ha) of all species combined, or foraging guild or individual species. The three principal guilds were trunk-bark foragers (species typically foraging on tree trunks or large branches), ground-shrub foragers (species typically foraging on or < 2 m above ground level), and sallier-canopy foragers (species typically foraging > 2 m above ground level in vegetation) (Yahner 1986, 1993).

I also derived an importance value (*IV*) for each species per season (winters or breeding seasons combined) as a means of comparing the importance of a given species in period 2 to the total bird community (Yahner 1993). An *IV* was the sum of a relative numerical component (*RN*) and a relative distribution component (*RD*). *RN* was the abundance (total number of contacts) of a given species at the 90 plots pooled from the two winters or the three breeding seasons and divided by the abundance recorded for the most abundant species. Maximum abundance was 32 contacts for Black-capped Chickadees (scientific names are given in Tables 2 and 4) in winter and 110 contacts for Ovenbirds in the breeding season ($\times 100$). *RD* was the proportion of the nine plot types in which a given species was observed during winters or breeding seasons combined ($\times 100$). I summed *RN* and *RD* (max. = 200) to classify a species as being of high ($IV \geq 125$), moderate (50–124), or low importance (≤ 49) in winter or the breeding season.

I compared observed versus expected numbers of contacts of all species combined, of each foraging guild, and of each species among the three sectors in period 2, using *G*-tests for goodness-of-fit (Sokal and Rohlf 1995, after Yahner 1993). If observed versus expected numbers of a given bird variable differed among sectors, I then used *a posteriori G*-tests for goodness-of-fit about the cell (i.e., sector) of interest. Observed versus expected numbers of contacts were also examined among plots within forested corridor and patch sectors if sample sizes were adequate to meet assumptions of the test. Expected numbers of contacts were obtained by multiplying the number of contacts of all species combined, guild, or individual species by the proportion of total number of plots per sector or plot type.

In addition, I compared observed versus expected numbers of contacts of all species combined, each foraging guild, and each species in a given sector or plot type immediately after the third cycle (period 1) (Yahner 1993, 1994) to numbers found in the present study (period 2) using *G*-tests for goodness-of-fit. Expected numbers of contacts were obtained by summing the total number of contacts obtained in a given sector or plot type in both periods 1 and 2 and dividing by 2. In all analyses, data were pooled by seasons (winter or breeding) to give a better measure of habitat-use patterns within and between periods and to increase sample size for statistical analyses (after Rice et al. 1984; Yahner 1986, 1993).

RESULTS

Spatial differences among sectors in winter (Period 2).—I observed 12 bird species in winters 1993–94 and 1994–95 combined at the Barrens Grouse HMA (Table 1). Most species (67%) were trunk-bark foragers,

TABLE 2

ABUNDANCE (*N*, NO./10 HA) OF INDIVIDUAL SPECIES IN THREE SECTORS OF FOREST MANAGEMENT AND IMPORTANCE COMPONENTS (*IV*, *RN*, *RD*) OF INDIVIDUAL SPECIES IN THREE SECTORS POOLED AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING WINTERS 1993–94 AND 1994–95 COMBINED (PERIOD 2)

	Sector				
Classification: Species[a]	Contiguous forest	Forested corridor	Forested patch	Total	*IV* (*RN*, *RD*)[b]
High importance:					
Black-capped Chickadee (*Parus atricapillus*)[c]	0.0[d]	5.7	8.4	6.3	144 (100, 44)
Moderate importance:					
Tufted Titmouse (*Parus bicolor*)	8.8	3.5	0.9	2.9	91 (47, 44)
Blue Jay (*Cyanocitta cristata*)	5.3	1.8	1.8	2.2	90 (34, 56)
Ruffed Grouse (*Bonasa umbellus*)	7.1	0.9	0.0	1.2	75 (19, 56)
Golden-crowned Kinglet (*Regulus satrapa*)	12.4	0.9	0.0	1.8	72 (28, 44)
White-breasted Nuthatch (*Sitta carolinensis*)	5.3	3.5	0.4	2.4	82 (38, 44)
Low importance:					
Downy Woodpecker (*Picoides pubescens*)	1.8	1.8	0.0	1.0	38 (16, 22)
Hairy Woodpecker (*P. villosus*)	0.0	2.2	0.0	1.0	38 (16, 22)
Northern Cardinal (*Cardinalis cardinalis*)	0.0	0.4	0.0	0.2	14 (3, 11)
Pileated Woodpecker (*Dryocopus pileatus*)	0.0	0.4	0.0	0.2	14 (3, 11)
Eastern Wild Turkey (*Meleagris gallopavo*)	3.5	0.0	0.0	0.4	17 (6, 11)
Red-bellied Woodpecker (*Centurus carolinus*)	0.0	0.0	0.4	0.2	14 (3, 11)

[a] Classification of bird species was based arbitrarily on *IV* values: high importance, $IV \geq 125$; moderate importance, $IV = 50–124$; low importance, $IV \leq 49$.

[b] Importance components: $IV = RN + RD$, where *RN* = the relative numerical component and *RD* = the relative distribution component.

[c] Observed versus expected number of contacts varied significantly among sectors: $G \geq 5.99$, $df = 2$, $P \leq 0.05$; *G*-test for goodness-of-fit.

[d] Observed number of contacts in this sector was significantly less than expected: $G \geq 3.81$, $df = 1$, $P \leq 0.05$, *G*-test for goodness-of-fit.

and *N* of trunk-bark foragers was nearly four-fold that of ground-shrub foragers (15.7 vs 4.0 individuals/10 ha, respectively). More species ($S = 10$) were noted in the forested corridor sector than in either the contiguous forest sector ($S = 4$) or the forested patch sector ($S = 8$). In addition, *N* of all species combined was higher in the forested corridor sector (21.2 individuals/10 ha) than in the other sectors (contiguous forest = 14.1 individuals/10 ha, forested patch = 19.5 individuals/ha).

The Black-capped Chickadee was the most common wintering species and was the only species classified as being of high importance ($IV \geq 125$) to the wintering bird community (Table 2). Abundance of chickadees varied among sectors, with fewer contacts in the contiguous forest compared to either forested corridor or patch sectors. Five species in decreasing order of abundance and of moderate importance ($IV = 50–124$) were Tufted Titmice, White-breasted Nuthatches, Blue Jays, Golden-crowned Kinglets, and Ruffed Grouse; although not significant ($P > 0.05$), abundances of each of these five species tended to be higher in the contiguous forest sector than in the other two sectors.

Spatial differences among plot types in winter (period 2).—Use of the four plot types by all species combined was significantly different in the forested corridor sector ($G = 25.5$, df = 3, $P < 0.005$). Clearcut plot types (plots A and B) were used less than expected ($G = 9.3$, df = 1, $P < 0.001$), whereas an uncut type (plot C) was used more than expected ($G = 13.0$, df = 1, $P < 0.005$). Abundance of trunk-bark foragers differed among plot types ($G = 36.7$, df = 3, $P < 0.005$), with significantly fewer contacts in recent clearcut plots (plots A and B) ($G \geq 12.0$, df = 1, $P < 0.005$) versus more contacts in uncut plots (plots C and D) ($G \geq 3.9$, df = 1, $P < 0.05$).

Use of plot types by all species combined also varied significantly in the forested patch sector ($G = 58.9$, df = 3, $P < 0.005$). The most recent clearcut plot (plot C) was used less than expected, but the uncut plot (plot D) was used more than expected ($G \geq 18.8$, df = 1, $P < 0.005$).

Spatial differences among sectors in the breeding season (period 2).—I recorded 40 species during the three breeding seasons combined (1993–95) at the Barrens Grouse HMA (Table 3). Compared to winter, most breeding species ($S = 21$, 53%) were ground-bark foragers; the remaining species were sallier-canopy ($S = 12$, 30%) and trunk-bark foragers ($S = 7$, 17%). Nearly all breeding species ($S = 37$) were noted in the forested corridor sector compared to fewer in forested patch ($S = 32$) and contiguous forest ($S = 15$) sectors. Ground-shrub foraging species occurred principally in the forested corridor and patch sectors ($S = 20$ and 18, respectively), with few in the contiguous forest sector ($S = 3$); conversely, S of both trunk-bark and sallier-canopy guilds was relatively similar among sectors ($S = 4–5$ and 7–10, respectively).

Abundance of all species combined tended to be lower ($0.10 > P > 0.05$) in the contiguous forest sector than in other sectors (Table 3). Abundance of ground-shrub foragers was significantly less than expected in the contiguous forest sector and greater than expected in the forested patch sector. Conversely, N of sallier-canopy foragers was higher than expected in contiguous forest and forested corridor sectors but lower in the forested patch sector.

Five (13%) of the 40 breeding species were categorized as being highly important to the breeding bird community, including Ovenbirds, Eastern Towhees, Common Yellowthroats, Red-eyed Vireos, and Rose-breasted

TABLE 3

SPECIES RICHNESS (*S*) AND ABUNDANCE (*N*, NO./10 HA) OF ALL SPECIES COMBINED AND OF THREE MAJOR FORAGING GUILDS IN THREE SECTORS OF FOREST MANAGEMENT AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING BREEDING SEASONS 1993–95 COMBINED (PERIOD 2)

	Sector			
	Contiguous forest	Forested corridor	Forested patch	Total
Species richness, *S*:				
All species combined	15	37	32	40
Trunk-bark foragers	4	6	5	7
Ground-shrub foragers	3	20	19	21
Sallier-canopy foragers	8	11	8	12
Abundance, *N*:				
All species combined	74.3	95.5	97.3	93.9
Trunk-bark foragers	7.1	8.0	10.3	8.9
Ground-shrub foragers[a]	24.8[b]	57.5	76.4[c]	62.2
Sallier-canopy foragers[a]	42.4[c]	30.0[c]	10.6[c]	22.8

[a] Observed versus expected number of contacts varied significantly among sectors; $G \geq 5.99$, df = 2, $P \leq 0.05$; *G*-test for goodness-of-fit.

[b] Observed number of contacts in this sector was significantly greater than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$; *G*-test for goodness-of-fit.

[c] Observed number of contacts in this sector was significantly less than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$; *G*-test for goodness-of-fit.

Grosbeaks (Table 4). Fourteen (35%) and 21 (52%) species were of moderate or low importance, respectively. Eleven (28%) breeding species varied significantly among the three sectors. For instance, abundance of Red-eyed Vireos was significantly higher than expected in the contiguous forest sector versus lower in the forested patch sector. Furthermore, some less common species, including Eastern Wood-Pewees, Downy Woodpeckers, Blue-gray Gnatcatchers, and Least Flycatchers tended to be more abundant in the contiguous forest than in either the forested corridor or the forested patch sector. Brown-headed Cowbirds, American Redstarts, and Baltimore Orioles predominated in the forested corridor sector. In contrast, abundances of size ground-shrub foragers, including Ovenbirds, Eastern Towhees, Common Yellowthroats, Gray Catbirds, Black-and-white Warblers, and Golden-winged Warblers, were most common in the forested patch sector.

Spatial differences among plot types in the breeding season (period 2).—Abundances of all species combined and of ground-shrub foragers differed among plot types in the forested corridor sector ($G \geq = 79.6$, df = 3, $P < 0.005$), with the most recent clearcut plot (plot B) used more than expected and the other three plot types used less than expected (*G*

TABLE 4

ABUNDANCE (*N*, NO./10 HA) OF INDIVIDUAL SPECIES IN THREE SECTORS OF FOREST MANAGEMENT AND IMPORTANCE COMPONENTS (*IV, RN, RD*) OF INDIVIDUAL SPECIES IN THREE SECTORS POOLED AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING BREEDING SEASONS 1993–95 COMBINED (PERIOD 2)

Classification: Species[a]	Sector: Contiguous forest	Sector: Forested corridor	Sector: Forested patch	Total	*IV (RN, RD)*[b]
High importance:					
Ovenbird (*Seiurus aurocapillus*)[d]	17.7	10.0[e]	18.0[f]	14.4	200 (100, 100)
Eastern Towhee (*Pipilo erythrophthalmus*)[d]	0.0[e]	8.8	15.0[f]	10.6	163 (74, 89)
Common Yellowthroat (*Geothlypis trichas*)[d]	0.0[e]	9.1	9.4[f]	8.3	135 (57, 78)
Red-eyed Vireo (*Vireo olivaceus*)[d]	17.7[f]	6.0	4.4[e]	6.6	134 (45, 89)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	4.7	6.5	3.2	4.8	134 (34, 100)
Moderate importance:					
Gray Catbird (*Dumetella carolinensis*)[d]	0.0[e]	7.8	10.0[f]	7.9	122 (55, 67)
Chestnut-sided Warbler (*Dendroica pensylvanica*)[d]	0.0[e]	5.0	6.2	5.0	90 (34, 56)
Black-and-white Warbler (*Mniotilta varia*)[d]	0.0	2.4	5.6[f]	3.5	103 (25, 78)
Golden-winged Warbler (*Vermivora chrystoptera*)[d]	0.0	0.3[e]	6.8[f]	3.1	67 (23, 44)
Brown-headed Cowbird (*Molothrus ater*)[d]	5.9	5.3[f]	0.3[e]	3.1	90 (23, 67)
American Redstart (*Setophaga ruticilla*)[d]	3.5	5.3[f]	0.0[e]	2.8	75 (19, 56)
Field Sparrow (*Spizella pusilla*)	0.0	2.4	3.2	2.5	61 (17, 44)
Black-capped Chickadee (*Parus atricapillus*)	1.2	2.9	2.1	2.4	105 (16, 89)
Tufted Titmouse (*P. bicolor*)	2.4	1.5	1.5	1.6	78 (11, 67)
Wood Thrush (*Hylocichla mustelina*)	0.0	2.4	1.2	1.6	67 (11, 56)
Baltimore Oriole (*Icterus galbula*)[d]	0.0	5.0[f]	0.0[e]	2.2	48 (15, 33)
Eastern Wood-Pewee (*Contopus virens*)	7.1	2.4	0.0	1.8	46 (13, 33)

TABLE 4
CONTINUED

Classification: Species[a]	Sector: Contiguous forest	Sector: Forested corridor	Sector: Forested patch	Total	*IV* (*RN*, *RD*)[b]
Downy Woodpecker (*Picoides pubescens*)	2.4	0.3	0.9	0.8	38 (5, 33)
Blue-gray Gnatcatcher (*Polioptila caerulea*)	2.4	0.9	0.3	0.8	49 (5, 44)
Indigo Bunting (*Passeria cyanea*)	0.0	0.6	1.2	0.8	38 (5, 33)
Least Flycatcher (*Empidonax minimus*)	3.5	0.0	0.3	0.5	26 (4, 22)
Ruffed Grouse (*Bonasa umbellus*)	0.0	0.6	0.6	0.5	48 (4, 44)
Cedar Waxwing (*Bombycilla cedrorum*)	0.0	1.2	0.0	0.5	15 (4, 11)
Yellow-billed Cuckoo (*Coccyzus americanus*)	0.0	0.3	0.6	0.4	36 (3, 33)
Nashville Warbler (*Vermivora ruficapilla*)	0.0	0.3	0.6	0.4	36 (3, 33)
Worm-eating Warbler (*Helmitheros vermivorus*)	0.0	0.3	0.6	0.4	36 (3, 33)
Chipping Sparrow (*Spizella passerina*)	0.0	0.3	0.03	0.3	24 (2, 22)
White-breasted Nuthatch (*Sitta carlinensis*)	0.0	0.6	0.0	0.3	13 (2, 11)
Pine Warbler (*Dendroica pinus*)	0.0	0.3	0.3	0.3	24 (2, 22)
Common Grackle (*Quiscalus quiscula*)	0.0	0.3	0.3	0.3	24 (2, 22)
Brown Thrasher (*Toxostoma rufum*)	0.0	0.0	0.6	0.3	13 (2, 11)
American Crow (*Corvus bachyrhynchos*)	0.0	0.3	0.3	0.3	13 (2, 11)
American Goldfinch (*Carduelis tristis*)	0.0	0.3	0.3	0.3	24 (2, 22)
Hairy Woodpecker (*Picoides villosus*)	1.2	0.3	0.0	0.3	24 (2, 22)
Yellow-throated Vireo (*Vireo flavifrons*)	0.0	0.3	0.0	0.1	12 (1, 11)
Red-bellied Woodpecker (*Centurus carolinus*)	0.0	0.0	0.3	0.1	12 (1, 11)

[a] Classification of bird species was based arbitrarily on *IV* values: high importance, $IV \geq 125$; moderate importance, $IV = 50–124$; low importance, $IV \leq 49$.
[b] Importance components: $IV = RN + RD$, where RN = the relative numerical component and RD = the relative distribution component.
[c] Observed versus expected number of contacts varied significantly among sectors; $G \geq 5.99$, df = 2, $P \leq 0.05$; *G*-test for goodness-of-fit.
[d] Observed number of contacts in this sector was significantly greater than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$; *G*-test for goodness-of-fit.
[e] Observed number of contacts in this sector was significantly less than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$; *G*-test for goodness-of-fit.

TABLE 5

PERCENT CHANGE (+ OR −) IN SPECIES RICHNESS AND ABUNDANCE OF ALL SPECIES COMBINED, FORAGING GUILDS, AND INDIVIDUAL SPECIES IN THREE SECTORS OF FOREST MANAGEMENT AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, FROM WINTERS 1988–90 (PERIOD 1) TO WINTERS 1993–95 (PERIOD 2). ONLY GUILDS OR INDIVIDUAL SPECIES WITH A SIGNIFICANT CHANGE IN ONE OR MORE SECTORS AND WITH >10 TOTAL CONTACTS IN A GIVEN SECTOR ARE PRESENTED

	Sector			
Classification:	Contiguous forest	Forested corridor	Forested patch	Total
Species richness	0.0	0.0	+14.3	+9.0
Abundance				
All species combined		+9.0	+51.7	+23.5
Trunk-bark foragers		+32.3	+66.7	+37.9[a]
Tufted Titmouse				+225.0[a]
White-breasted Nuthatch				+200.0[a]
Blue Jay				+266.7[a]

[a] Observed abundance was significantly different from expected during winters 1988–89 and 1989–90 combined versus winters 1993–94 and 1994–95 combined; $G \geq 3.81$, df = 1, $P < 0.05$. G-test for goodness-of-fit.

≥ 4.1, df = 1, $P < 0.05$). Use of plot types by towhees, yellowthroats, and catbirds also varied in the forested corridor sector ($G \geq 14.2$, df = 3, $P < 0.001$). Abundances of each of these three species were greater than expected in plot B but less than expected in plot C ($G \geq 4.3$, df = 1, $P < 0.05$).

Abundances of all species combined, of ground-shrub foragers, and of sallier-canopy foragers differed among plot types in the forested patch sector ($G \geq = 13.1$, df = 3, $P < 0.005$). Older plots (plots A and D) were used less than expected, and the most recent clearcut plots (plot C) were used more than expected by all species combined and by ground-shrub foragers ($G \geq 4.1$, df = 1, $P < 0.05$). In contrast, sallier-canopy foragers used the two most recent clearcut plots (plots B and C) less than expected but used the uncut plots (plot D) more than expected ($G \geq 4.4$, df = 1, $P < 0.05$). Some examples of differential use of plot types by individual species in the forested patch sector were less than expected use of plot C by Ovenbirds versus greater than expected use of plot C by catbirds, Chestnut-sided Warblers, and Golden-winged Warblers ($G \geq 6.2$, df = 1, $P < 0.005$).

Temporal trends in winter (periods 1 vs 2).—Species richness increased slightly (9.0% increase) from period 1 to period 2 at the Barrens Grouse HMA, with a change observed only in the forest patch sector (Table 5). However, abundances of trunk-bark foragers increased nearly 38% from

TABLE 6

PERCENT CHANGE (+ OR −) IN SPECIES RICHNESS AND ABUNDANCE OF ALL SPECIES COMBINED, FORAGING GUILDS, AND INDIVIDUAL SPECIES IN FOUR PLOT TYPES EACH OF THE FORESTED CORRIDOR AND PATCH SECTORS AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, FROM WINTERS 1988–90 (PERIOD 1) TO WINTERS 1993–95 (PERIOD 2)[a]

Sector	Type			
	Plot A	Plot B	Plot C	Plot D
Forested corridor:				
Species richness	−50.0	−33.3	+75.0	−42.9
Abundance				
All species combined	−66.7[a]		+420.0[a]	−36.0
Forested patch:				
Species richness	0.0	+33.3	−50.0	+40.0
Abundance				
All species combined	−50.0	+175.0		+216.7[b]
Trunk-bark foragers		+266.7[b]	+340.0[b]	+91.7
Black-capped Chickadee		+900.0[a]		+50.0

[a] Only guilds or individual species with a significant change in one or more sectors and with >10 total contacts in a given sector are presented.

[b] Observed number of contacts was significantly different from expected in winters 1988–89 and 1989–90 combined versus winters 1993–94 and 1994–95 combined; $G \geq 3.81$, df = 1, $P \leq 0.05$; G-test for goodness-of-fit.

period 1 to period 2; in addition, *N* of Tufted Titmice, White-breasted Nuthatches, and Blue Jays increased at least 200% from period 1 to 2.

In the forested corridor sector, richness and abundances of all species combined increased from period 1 to period 2 in plot C but not in the other three plot types (Table 6). Also, *N* of all species combined declined significantly in the oldest clearcut plots (plot A). In the forested patch sector, *S* increased in two plot types (plots B and D) but decreased in the most recent clearcut plots (plot C) from period 1 to period 2. Moreover, *N* of all species in uncut types (plot D), of trunk-bark foragers in the two most recent clearcut types (plots B and C), and of Black-capped Chickadees in plot B increased between periods in the forested patch sector.

Temporal trends in the breeding season (periods 1 vs 2).—As in winter, *S* in the breeding season increased slightly (+5.3%) from periods 1 to 2, especially in both forested corridor and patch sectors (Table 7). Abundances of all species combined, of sallier-canopy foragers, and of five species (e.g., Ovenbirds) at the Barrens Grouse HMA increased significantly from period 1 to 2, whereas *N* of Common Yellowthroats, Scarlet Tanagers, and Indigo Buntings declined significantly between periods. In the forested corridor sector, *N* of Ovenbirds, Red-eyed Vireos, and Brown-

TABLE 7

PERCENT CHANGE (+ OR −) IN SPECIES RICHNESS AND ABUNDANCE OF ALL SPECIES COMBINED, FORAGING GUILDS, AND INDIVIDUAL SPECIES IN THREE SECTORS OF FOREST MANAGEMENT AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, FROM WINTERS 1988–90 (PERIOD 1) TO WINTERS 1993–95 (PERIOD 2)[a]

	Sector			
Classification:	Contiguous forest	Forested corridor	Forested patch	Total
Species richness	+14.2	+19.3	−12.5	+5.3
Abundance				
All species combined	+8.6	+37.3[b]	+4.1	+17.3[b]
Ground-shrub foragers	+16.7	+30.0[b]	+0.8	+11.8
Sallier-canopy foragers	+20.0	+75.9[b]	+2.9	+40.3[b]
Ovenbird	+36.4	+325.0[b]	+144.0[b]	+150.0[b]
Common Yellowthroat		0.0	−44.8[b]	−29.2[b]
Red-eyed Vireo	+36.4	+122.2[b]	+25.0	+56.3[b]
Rose-breasted Grosbeak		+83.3	+37.5	+85.0[b]
Black-and-white Warbler		+166.7	+137.5[a]	+125.0[b]
Brown-headed Cowbird		+260.0[b]		+118.2[b]
Field Sparrow			−56.0[a]	−42.4
Scarlet Tanager		−36.4	−57.1	−54.2[b]
Indigo Bunting	−50.0	−81.8		−216.7[b]

[a] Only guilds or individual species with a significant change in one or more sectors and with >10 total contacts in a given sector are presented.
[b] Observed number of contacts was significantly different from expected in breeding seasons 1988–90 combined versus breeding seasons 1993–95 combined; $G \geq 3.81$, df = 1, $P \leq 0.05$; G-test for goodness-of-fit.

headed Cowbirds increased significantly between periods; in the forested patch sector, *N* of Black-and-white Warblers increased while those of Common Yellowthroats and Field Sparrows decreased.

In the forested corridor sector, *S* showed the greatest change in the most recent clearcut plots (plot B, +28.6%) from period 1 to 2 (Table 8). Similarly, I found significant increases in *N* of all species combined, ground-shrub foragers, sallier-canopy foragers, Gray Catbirds, Chestnut-sided Warblers, and cowbirds in plot B between periods. In contrast, abundance of Ovenbirds increased but that of ground-shrub foragers in general declined in the oldest clearcut plots (plot A).

In the forested patch sector, *S* increased primarily in the two most recent types of clearcut plots (plots B and C) from period 1 to 2 (Table 8). I observed significant increases in *N* between periods with all species combined, ground-shrub foragers, catbirds, and Golden-winged Warblers in plot C and with Ovenbirds in the two older clearcut plots (plots A and B). Conversely, *N* of ground-shrub foragers and catbirds declined in the oldest clearcut plot (plot A) while that of yellowthroats decreased in plot B.

TABLE 8

PERCENT CHANGE (+ OR −) IN SPECIES RICHNESS AND ABUNDANCE OF ALL SPECIES COMBINED, FORAGING GUILDS, AND INDIVIDUAL SPECIES IN FOUR PLOT TYPES EACH OF THE FORESTED CORRIDOR AND PATCH SECTORS AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, FROM BREEDING SEASONS 1988–90 (PERIOD 1) TO BREEDING SEASONS 1993–95 (PERIOD 2)[a]

	Type			
Sector	Plot A	Plot B	Plot C	Plot D
Forested corridor:				
Species richness	+5.3	+28.6	−19.0	+17.6
Abundance				
All species combined	−21.5	+113.8[b]	−10.0	+100.0[b]
Ground-shrub foragers	−35.7[b]	+88.1[b]	−8.0	+133.3[b]
Sallier-canopy foragers	+20.0	+218.2[b]	+14.3	+73.3
Ovenbird	+233.3[b]	+166.7		+550.0[b]
Gray Catbird		+300.0[b]		
Chestnut-sided Warbler		+275.0[b]		
Brown-headed Cowbird		+400.0[b]		
Forested patch:				
Species richness	0.0	+42.9	+45.5	+5.9
Abundance				
All species combined	−22.4	−13.3	+59.0[b]	−17.1
Ground-shrub foragers	−31.4[b]	−18.5	+48.3[b]	−18.4
Sallier-canopy foragers				
Ovenbird	+120.0[b]	+750.0[b]		+46.2
Common Yellowthroat	−55.6	−83.9[b]	+29.4	
Gray Catbird	−81.3[b]	+8.3	+1700.0[a]	
Golden-winged Warbler		−25.0	+200.0[a]	

[a] Only guilds or individual species with a significant change in one or more sectors and with >10 total contacts in a given sector are presented.

[b] Observed number of contacts was significantly different from expected in breeding seasons 1988–90 combined versus breeding seasons 1993–95 combined: $G \geq 3.81$, df = 1, $P \leq 0.05$; G-test for goodness-of-fit.

DISCUSSION

Wintering bird community dynamics.—I noted at least five trends in the community structure of wintering birds on my study site in central Pennsylvania from 1988–95. First, abundances of all species combined and of the two foraging guilds (trunk-bark and ground-shrub foragers) did not differ among sectors (contiguous forest, forested corridor, and forested patch) for nearly a decade after the third cutting cycle (Yahner 1993, present study). This supports the contention that species richness and population abundances of wintering birds are generally less affected by small-scale forest clearcutting than breeding birds (Yahner 1985, Maurer and Heywood 1993).

A second trend was the continued high abundance of wintering trunk-bark foragers relative to ground-bark foragers at the Barrens Grouse HMA (e.g., Yahner 1993), which may be related to the availability of foraging substrate for these guilds in winter. Rough-barked trees (e.g., *Quercus*) were common in uncut plot types throughout the study site (Yahner 1987). These types of trees are important as foraging substrate because of numerous crevices for arthropods that serve as an important food for trunk-bark foragers (Brawn et al. 1982, Morrison et al. 1985). I attribute the relative lack of wintering ground-shrub foragers to a paucity of weed seeds as a food resource (Yahner 1986, 1993). Weedy, herbaceous vegetation was mainly restricted to habitat immediately adjacent to the unimproved road bisecting the study site (Fig. 1). In contrast, ground-shrub foragers, e.g., White-throated Sparrows (*Zonotrichia albicollis*), were quite common in winter at nearby (<10 km) irrigated forested stands where herbaceous vegetation was abundant (Rollfinke and Yahner 1990).

A third trend in the wintering bird community was greater use of older plots (e.g., plot C in the forested corridor sector) and lesser use of more recent clearcut plots (e.g., plot C in the forested patch sector) subsequent to both second and third cutting cycles (Yahner 1987, 1993; present study). Interiors of uncut plots likely provided a better microclimate for wintering birds (Ranney et al. 1981) and, therefore, reduced the energetic costs associated with foraging (Morrison et al. 1986, Yahner 1987).

A fourth trend in winter at the Barrens Grouse HMA was the common occurrence of Black-capped Chickadees in both periods (Yahner 1986, 1993; present study). This species is very common in managed stands throughout the eastern deciduous forests during winter (e.g., Conner et al. 1979, Rollfinke and Yahner 1990). Moreover, perhaps chickadees were particularly abundant in the intermediate-aged clearcut plot (plot B) in the forested patch sector during period 2 because of plant succession; for example, the density of understory stems in plot B of this sector increased 71% from period 1 to 2 (Yahner, unpubl. data). In winter, Black-capped Chickadees prefer to forage on small woody stems in the understory (Brawn et al. 1982, Morrison et al. 1985).

A final trend in the wintering bird community were greater abundances of three species (titmice, nuthatches, and jays) in period 2 than in period 1, which may also be partially explained by plant succession and regional population increases. The density of overstory trees in clearcut plot types in forested corridor and patch sectors combined increased 79% from periods 1 to 2 (Yahner, unpubl. data), thereby providing more foraging substrate for trunk-bark foragers, such as titmice and nuthatches. Although mast production was not measured in my study, a greater density of overstory trees between periods probably increased mast availability, which is an important winter food resource for Blue Jays (Smith 1986). Furthermore, each of these three species has shown a general population increase in central Pennsylvania (e.g., Allegheny Plateau) over the past few decades (Wiedenfeld et al. 1992).

Breeding bird community dynamics.—I noted six trends in the community structure of breeding birds on the managed forested landscape in central Pennsylvania. First, richness of all species combined tended to be much higher on both forested corridor and patch sectors than on the contiguous forest sector; a higher S on managed versus reference (uncut) forested landscapes is also reported on this study site prior to period 2 (Yahner 1986, 1993) and in other studies of breeding bird communities (e.g., Welsh and Healy 1993). However, I caution that a lower S on the contiguous forest sector may be attributed in part to a reduced sampling effort on the reference than on the treated area of the Barrens Grouse HMA (see Conner and McCoy 1979).

Second, although abundance of all species combined did not vary among the three sectors for several years since the third cutting cycle at the Barrens Grouse HMA, abundances of the two major guilds, i.e., ground-shrub and sallier-canopy foragers, differed among sectors as a probable consequence of forest management (Yahner 1993; present study). Ground-shrub foragers, which represented the principal guild in both periods, were most common in the forested patch sector because of the creation of considerable amounts of edge and brushy habitat via clearcutting. Conversely, sallier-canopy foragers occurred mainly in the other two sectors (contiguous forest and forested corridor) in period 2 because of abundant overstory trees as foraging substrate (e.g., Yahner 1987); furthermore, recent clearcut plots (plot B) in the corridor sector were used extensively by sallier-canopy foragers in possible response to the retention of residual trees (Yahner 1995).

Third, in terms of population abundances, five ground-shrub foraging species in period 2 were positively affected by forest clearcutting; these included towhees, catbirds, yellowthroats, Black-and-white Warblers, and Golden-winged Warblers. A similar response by these species to clearcutting has been noted in other studies (e.g., Crawford et al. 1981; Yahner 1986, 1993; Thompson et al. 1992). These species were found mainly in the most recent clearcut plots which contained dense, brushy vegetation near ground level compared to uncut plots at the Barrens Grouse HMA (Yahner, unpubl. data). The towhee is an example of a brush-inhabiting species whose populations are doing quite well at the Barrens Grouse HMA (Lewis 1996) but have shown declines in recent years as a plausible result of forest maturation throughout much of the Northeast (e.g., Hagan 1993). Common Yellowthroats and Golden-winged Warblers also have exhibited population declines over the past few decades in eastern North America (James et al. 1996). My findings, therefore, confirm the importance of disturbed habitats, such as small clearcut plots, to long-term trends in populations of early-successional species (DeGraaf et al. 1993, Litvaitis 1993, Yahner 1995). In addition, nesting success of species for which data from the Barrens Grouse HMA are available (e.g., catbirds, towhees, yellowthroats, and Wood Thrushes) is comparable to those reported in other modified landscapes (see Yahner 1991, Yahner and Ross 1996).

A fourth trend in the breeding bird community at the Barrens Grouse HMA was the recent increase in abundance of the Ovenbird since period 1, whereas the Eastern Towhee was the predominant breeding species prior to period 2 (Yahner 1986, 1993). The Ovenbird was particularly common in the uncut plots of the highly fragmented forest patch sector, suggesting that Ovenbird populations on a localized basis may be unaffected by small-scale forest clearcutting (see Thompson et al. 1992, Yahner 1993). Some studies in more intensively fragmented landscapes, however, have contended that Ovenbirds are area-dependent and, hence, negatively affected by habitat fragmentation (e.g., Robbins et al. 1989). I have no data to confirm whether Ovenbirds using small (1-ha) plots in the forested patch sector had reduced reproductive success (e.g., Gibbs and Faaborg 1990, Donovan et al. 1995), although the frequency of paired Ovenbirds that were presumed to be mated did not vary ($P > 0.10$) among the three sectors at the Barrens Grouse HMA (Yahner, unpubl. data). On the other hand, Red-eyed Vireos and cowbirds were perhaps the only breeding species negatively affected by forest clearcutting. Abundance of vireos was higher in the contiguous forest sector than in other sectors during period 2. Other studies (e.g., Robbins et al. 1989, Thompson et al. 1992) have concluded that habitat fragmentation can negatively influence abundance and distribution of Red-eyed Vireos. The cowbird was possibly negatively affected by clearcutting with higher numbers of this species observed in forested corridor and contiguous forest sectors than in the forested patch sector during period 2. But this trend is not surprising because recent evidence has suggested that rates of cowbird parasitism in the Northeast may be locally higher in forest-interior than in forest-edge habitats (Hahn and Hatfield 1995).

A fifth trend was an increase in abundances of several species (e.g., Ovenbirds, Red-eyed Vireos, Black-and-white Warblers, and Rose-breasted Grosbeaks) from period 1 to 2 at the Barrens Grouse HMA, which may be in part be a consequence of plant successional changes (see Crawford et al. 1981, Yahner 1993). Of these species, populations of Red-eyed Vireos have increased significantly on a regional scale, based on trends confirmed by Breeding Bird Surveys in eastern North America from 1966–1991 (Peterjohn and Sauer 1994).

A sixth and opposite trend was a significant decline in population abundances of Common Yellowthroats, Scarlet Tanagers, Field Sparrows, and Indigo Buntings at the Barrens Grouse HMA from period 1 to 2. I attributed declines in yellowthroats and Field Sparrows to plant succession, whereby recent clearcut plots (e.g., plot B in the forested patch sector) in period 2 became less suitable as breeding habitat than in period 1 (see Yahner 1986, 1993). I have no explanation for declines in tanagers and buntings on my study site, but declines in Field Sparrows at the Barrens Grouse HMA may be related to significant declines in this species from 1966–91 throughout much of eastern North America (see Askins 1993).

Based on studies since the early 1980s at the Barrens Grouse HMA, I conclude the small-scale forest management has not resulted in a long-term, detrimental effect on bird communities. Forest fragmentation and subsequent plant succession, for instance, have had minimal impact on species richness of wintering and breeding bird communities in this managed forested landscape. Furthermore, abundances of bird species dependent on contiguous uncut forests were generally unaffected over the past several years, whereas abundances of early successional species were usually augmented by small-scale forest management.

Habitat management resulting in a combination of contiguous forest, corridors, and small patches, provides a variety of suitable conditions for both wintering and breeding bird communities. A managed landscape containing contiguous forest and forested strip corridors particularly benefits trunk-bark foragers in winter and sallier-canopy foragers in the breeding season. Furthermore, the retention of residual trees in clearcut plots is of value to sallier-canopy foraging species. When the landscape also contains a mosaic of small forested patches, ground-shrub foragers are positively affected in the breeding season, e.g., Eastern Towhees. However, as plant succession progresses on a managed landscape, such as that created for grouse habitat in central Pennsylvania, it likely will become less suitable for certain breeding species, such as Common Yellowthroats and Field Sparrows, that rely on recent clearcut plots. Hence, a variety of breeding bird species will occur if a continuum of plot types ranging from early successional to uncut forested plots is present in the managed forest landscape.

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